Pedobiologia, Bd. 13, S. 140—149 (1973)

Molslaboratoriet, Femmøller, Denmark

# Inhibitory effects of carbon dioxide on microbial activity in soil

A. Macfadyen[1])

With 5 figures

(Accepted 20. X. 1972)

## 1. Introduction

During a study of respiratory activity of a sandy soil under *Calluna vulgaris* (L.) Hull. in the research area of Molslaboratoriet, Denmark the possibility that metabolic activity might be limited by accumulation of carbon dioxide was suggested by failure of carbon dioxide output of the soil, as measured in the field, to reach expected maxima both on a diurnal and on a seasonal time-scale. A similar limiting affect appeared to occur during laboratory experiments with the same soil which were designed to measure the effect of temperature on total soil metabolism.

In these experiments, soil cores were kept in the laboratory in large sealed glass tanks with open water surfaces in order to maintain saturated conditions. The effect of temperature on the output of carbon dioxide followed an approximate $Q_{10} = 2$ relationship up to about 15 °C but at higher temperatures a threshold or ceiling level of carbon dioxide output was reached, beyond which no increase in respiration rate occurred. When, later, the samples were kept unconfined in a room, the humidity of which was controlled and when the vessels were only closed for the short duration of the actual carbon dioxide measurement period, the expected increases in the level of carbon dioxide output were measured as temperature was raised.

At a later stage, on searching the literature for information on the effect of carbon dioxide concentration on soil microbes, the work of Burges and Fenton (1953) was read. In this, the low tolerance of soil fungi normally found in sandy acid Breckland soils is demonstrated. Until that time the generally accepted dogma of the relative insensitivity of soil microbes to high carbon dioxide levels had been assumed.

An attempt was therefore made to determine the level at which the metabolism of the soil in question was affected by carbon dioxide in the laboratory, to determine whether such levels occur in practice in the field and to compare the behaviour of the sandy, acid Molslaboratoriet soils with other soils from different areas and with different properties.

## 2. Methods

(1) The simple technique for measuring soil carbon dioxide output from soil is describe fully elsewhere (Macfadyen, in prep.). The gas is absorbed in dilute alkali which contains an indicator and an excess of barium chloride. After an interval of one or two hours the alkali

1) The New University of Ulster, Coleraine, Northern Ireland.

is titrated with N/10 hydrochloric acid and the amount previously neutralised by the carbon dioxide is estimated.

(2) In an attempt to measure fairly precisely the influence of different carbon dioxide concentrations on soil metabolism a Warburg technique was applied to air-dried and ground soil samples which were then re-wetted. The metabolic history of such samples after re-wetting is well documented in the literature (e. g. see Birch and Friend 1956). A considerable burst of activity occurs immediately after the re-wetting which rapidly reaches a peak and subsequently decays rougly exponentially to a lower level.

Chase and Gray (1953) claimed that the decay curve is best fitted by the formula

$$Y = F'/t^{m'}$$

in which Y represents oxygen uptake in $\mu l/g/hr$, $F'$ and $m'$ are constants and $t$ is time in days.

Since this is equivalent to $\log Y = \log F' - m' \log t$, it follows that decay curve, if plotted logarithmically, should produce a straight line. In the case of the present experiments the peak was only reached after about ten days and nearly six weeks were required for a decline of the respiration rate to a lower asymptotic level.

Equal weights of such homogenised material, although differing greatly from fresh soil, have highly reproduceable metabolic activity patterns and permit close replication of metabolic experiments.

In the present experiments samples were derived from clearly defined soil horizons (L = Litter, F = Fermentation and H = Humus Layers) from beneath healthy growing *Calluna vulgaris* on a sandy soil at Lyngjorden in Molslaboratoriet area.

The material was dried at 40 °C for about four hours, left under cover from dust for six weeks at 10 °C, ground in a "flail type" electric grinder (Culotti) and kept for use in a cool dry place at less than 10 °C in polythene bags. No special aseptic precautions were taken. The water capacity of subsamples of the soil was determined by centrifuging for a quarter of an hour at 3,000 rpm in order to be able to bring the samples to 60 % saturation on re-wetting. Samples weighing from 0.15—1.0 g were wetted after being placed in the Warburg flasks and were stored in large closed glass vessels in the presence of excess N/10 potassium hydroxide solution (to prevent build up of carbon dioxide) at 10 °C before being used as standard test material. Preliminary measurements when in the presence of alkali were made over a period of three or four days and sets of samples were selected so that their initial respiration rates were closely similar. These were used as control and experimental samples. Characteristic values for each layer of the sandy soil from beneath *Calluna vulgaris* were, in units of $\mu l/g/hr$:

L layer (30), F layer (16), H layer (10), A horizon (10).

The samples were re-wetted and then subjected to known levels of carbon dioxide in the Warburg vessels; the level was maintained by means of carbon dioxide buffers (Macfadyen 1970) which replaced the normal potassium hydroxide solution in the well of the vessel. The flasks were initially flushed through with carbon dioxide/air mixtures prepared in a bell-jar over liquid paraffin to the same concentration. The composition of the mixture was measured in this gas at the start of the experiment and in the Warburg vessels (using the side arm) at the end of the experiment by means of the electrolytic syringe method already described (Macfadyen 1970). The calibration of flasks and all other procedures followed normal Warburg respirometer practice as described for instance by Umbreit et al. (1957).

The respiration rates of the soil samples were measured under the influence of a range of carbon dioxide concentrations from 0—10 % carbon dioxide. Controls were used and the experimental samples were returned to 0 % carbon dioxide levels afterwards.

Two possible effects of the carbon dioxide buffers, additional to their influence on carbon dioxide levels, were considered and tested by additional experiments. These were the desiccating effect of the ethanolamine and any toxic effect of the hydrochloric acid vapour which were contained in the mixtures. Buffers were only used which maintained a humidity above 90 % and toxic effects were eliminated experimentally by running control experiments subject to hydrochloric acid vapour. No depression of respiration was detected.

Forsyth and Eaves (1969) point out that buffers containing ethanolamine can produce ethylene in toxic quantities. This was not recognised at the time of the experiments but two points suggest that this effect is irrelevant to these results. Firstly ethylene production decreased in the order di-mono-tri-ethanolamine whilst in the experiments reported here it is the di-ethanolamine experiments which have least depression of respiration and the tri-ethanolamine ones which have most. Secondly a whole series of control samples, as reported further, showed no depression of respiration despite the use of the buffers.

When the level of carbon dioxide responsible for inhibition had been determined in the sandy Molslaboratoriet soils, other soils were subjected to the same treatment for comparison.

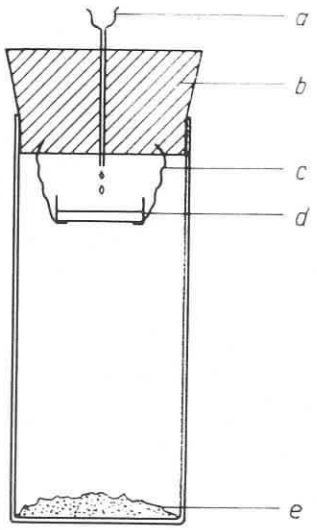


Fig. 1 Experiment on maximum carbon dioxide attained in a confined vessel. (The figure refers to the time of injection of the alkali.) (a) Hypodermic needle, (b) Stout rubber bung, (c) Wire loop, (d) Shallow dish to contain alkali, (e) Soil sample.

(3) As an independent check on the reality of the inhibition phenomenon, a simple laboratory experiment was conducted. In this, flat bottomed glass tubes of about 150 m*l* volume were fitted with a massive rubber bung from which a small (3 m*l*) glass dish was suspended in a wire loop. Air dried "soil" was placed in the bottom of the tube and re-wetted and the bung then inserted (Fig. 1). At successive intervals after enclosure the carbon dioxide content of the air in one of the tubes was measured. Excess alkali (containing indicator and barium chloride) was injected through the bung with a powerful hypodermic needle. After one hour the alkali was titrated and the amount of carbon dioxide absorbed calculated. From the knowledge of the volume of air enclosed in the tube the maximum percentage of carbon dioxide was calculated, it being assumed that no significant amount of fresh carbon dioxide had been emitted during the short absorption period.

(4) In order to check the relevance of the laboratory experiments to field conditions, two field techniques for sampling the carbon dioxide concentration of the soil atmosphere were devised, using thin walled polythene tubes which could be buried at known depths (MACFADYEN 1970) in one method the tubes were inflated with air and sympled by means of the electrolytic syringe technique. In the other the tubes contained sodium bicarbonate solution and the equilibrium concentration of carbon was calculated from the *p*H of the solution.

## 3. Results

### 3.1. Laboratory demonstration of a limiting respiration rate in enclosed, as compared with exposed soil cores

A total of twelve cylindrical soil cores, approximately 50 mm deep by 60 mm diameter were taken adjacent to one another from an area of soil beneath *Calluna vulgaris*. They were placed in a glass tank in a constant temperature room at 11 °C. After one week samples were moved to a series of different temperatures at intervals of several days and the rate of carbon dioxide production was measured before and after the move. The results are given in table 1 and fig. 2. For comparison, later experiments on soil from the same site but with samples left open in a room whose air was saturated with water vapour are indicated in the form a regression line. These show a simple $Q_{10} = 2$ relationship (MACFADYEN in prep.) which is drawn on the same figure.

Although these figures are not extensive they indicate the existence of some upper limit to the soil respiration rate, regardless of temperature. Such a ceiling might, of course, arise through accumulation of toxic products, exhaustion of nutrients or oxygen etc. However, it was argued that if respiration had involved the replacement, in a 20 *l*

Table 1 The succession of the mean respiration values (in mg $CO_2$ per sample per hour) obtained following movement to different temperatures

| Day after collection | 7 | 8 | 9 | 9 | 10 | 10 | 11 | 11 | 12 | 14 | 14 | 15 | 15 | 16 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Temperature °C | 6 | 6 | 6 | 11 | 11 | 15 | 15 | 21 | 21 | 21 | 16 | 16 | 21 | 21 |
| Respiration rate $\mu l$/hr | 256 | 215 | 227 | 633 | 577 | 514 | 500 | 686 | 705 | 473 | 579 | 430 | 547 | 499 |

Note. The samples were kept confined in a 20 litre container between measurements.

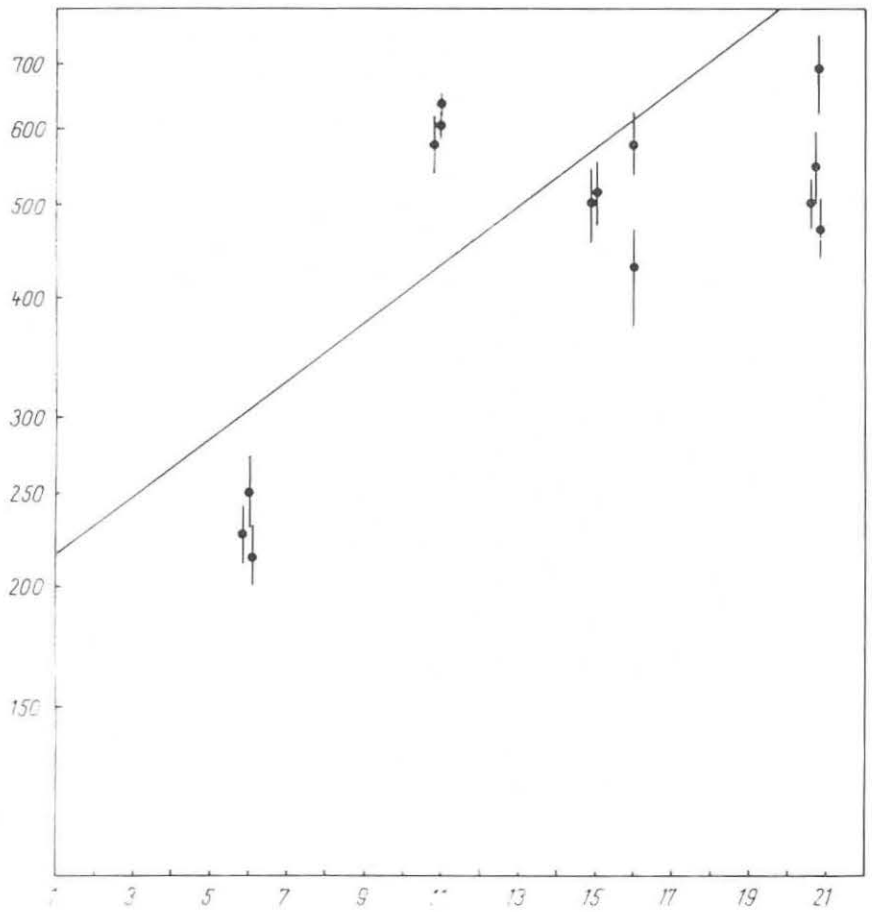


Fig. 2 Relation between temperature and carbon dioxide production of soil samples in a confined vessel. Results with confined samples are plotted as mean $\pm 5\%$ fiducial limits. The regression line was derived independently from samples not confined in a vessel. Abscissa Temperature °C. Ordinate respiration rate in arbitrary units. Log scale.

container, of about 1 *l* of oxygen by carbon dioxide during the course of a day; the change from 20% oxygen to 15% oxygen would have been proportionately less influential on the corresponding soil metabolism than a change from 0.03—5% carbon dioxide.

### 3.2. Respirometry of re-wetted "soil samples" in controlled atmosphered

Trial experiments on freshly re-wetted "soil" and with a buffer producing 2.5% carbon dioxide and 90% relative humidity indicated that respiration was entirely inhibited in a F layer sample (Fig. 3). This occurred within two days of exposure of the sample to the carbon dioxide buffer. A number of experiments were then carried out using a buffer solution producing 0.8% carbon dioxide. These indicated a reduction from about 4 or 5 m*l* per hour to a level of 1 – 2 m*l* per hour (Fig. 4). It was also shown that the re-

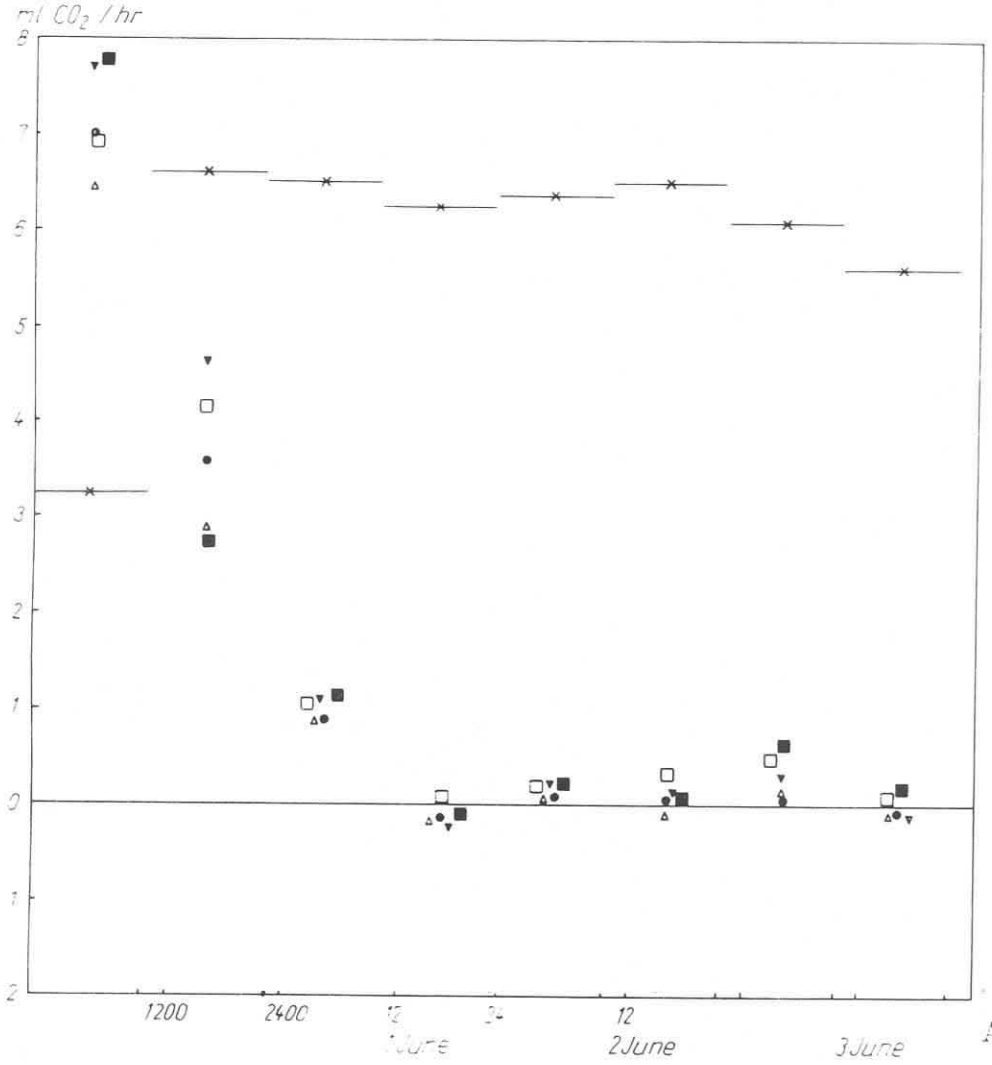
ml $CO_2$ / hr
8
7
6
5
4
3
2
1
0
1
2
1200
2400
12
12
2June
3June

Abb. 3

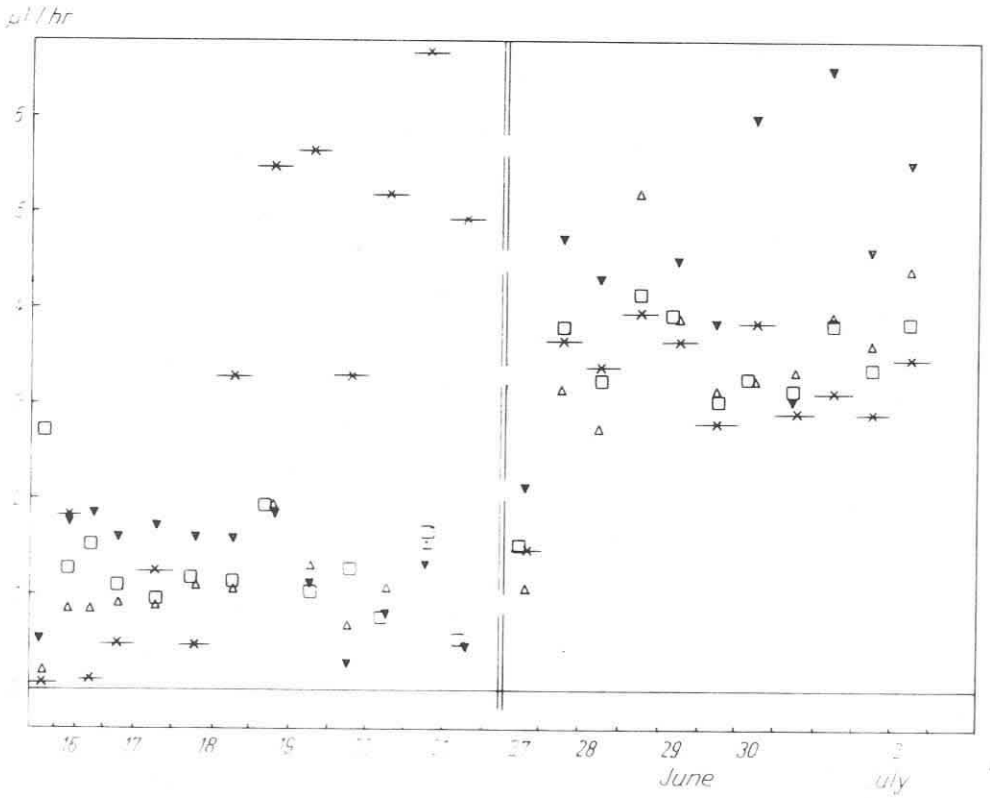
µl / hr
5
4
16
17
18
19
27
28
29
30
June

Abb. 4

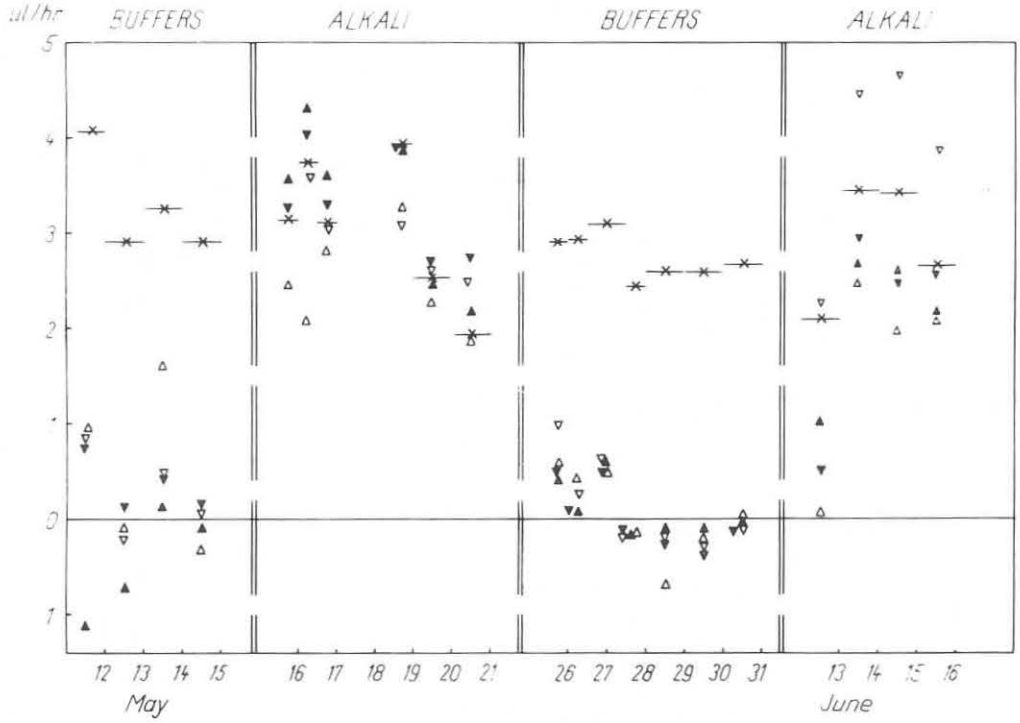


Fig. 5 Warburg experiment with two buffers similar to Fig. 4. Two flasks (upright triangles △) treated with higher $CO_2$ levels: 2.05% and 0.70% on the first and second occasions respectively. Two flasks (inverted triangles ▽) treated with lower levels: 0.88% and 0.25% respectively. In each case the change of buffer or alkali occurred in the preceeding twelve hour period. The readings after 21 May and 31 May are omitted for clarity; they continued the same pattern as on these dates. Abscissa: date. Ordinate: $CO_2$ evolution in $\mu l$/hr.

spiration rate of the sample returned to normal level when alkali was substituted for the buffer and the carbon dioxide level restored to zero. Similar recoveries occurred after complete suppression of respiration with buffers giving 2.5% carbon dioxide. More detailed experiments were then designed in which the carbon dioxide level of the controls and the experimentals was interchanged. F layer material with potassium hydroxide (0% carbon dioxide level) maintained a steady respiration level of between 4 and 5 $ml$ per hour. The remaining samples were subjected to variation of carbon dioxide level as shown in Fig. 5 and Table 2. It was concluded that on this occasion carbon dioxide levels of 0.7% and above completely inhibited respiration and that, even at 0.25% carbon dioxide respiration was extremely low. In fact the precise level at which inhibition occurred proved to vary considerably between different batches of samples.

---

Fig. 3 Warburg experiment with Buffer to give 2.5% $CO_2$. Control flask plots (x) show the duration of all measurements. Experimentals are plotted approximately in the middle of the experimental period but some are displaced in time for clarity. Each symbol represents a different experimental flask which was used continuously throughout the period of the experiment. Abscissa: Date. Ordinate: Rate of $CO_2$ evolution in $\mu l$/hr.

Fig. 4 Warburg experiment with Buffer to give 0.8% $CO_2$ plotting as for Fig. 3. The flasks were removed to a $CO_2$ free atmosphere on 21 June and replaced, using alkali instead of Buffer on 27 June. Each symbol represents a different experimental flask which was used continuously throughout the period of the experiment. Note depression to about 1 $\mu l$/hr in presence of buffer and return to normal in presence of alkali. Abscissa: date. Ordinate: $CO_2$ evolution in $\mu l$/hr.

Table 2 The effect of a range of carbon dioxide concentrations on the respiration rate of 1 g samples of re-wetted soil from the sandy *Calluna* soil. (Third series of experiments.)

| Date | 2 and 3 | | 5 and 8 | | 9 (Control) | | 6 and 7 | | 4 and 10 | | 11 (Control) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $CO_2$ | $O_2$ | $CO_2$ | $O_2$ | $CO_2$ | $O_2$ | $CO_2$ | $O_2$ | $CO_2$ | $O_2$ | $CO_2$ | $O_2$ |
| May 11 | 2.05 | 0.0 | 0.88 | 0.0 | 0 | 2.0 | 2.05 | 0.0 | 0.88 | 0.0 | 0 | 3.0 |
| 15 | 0.00 | 2.5 | 0.00 | 3.5 | 0 | 4.0 | 0.00 | 2.0 | 0.00 | 2.5 | 0 | 2.0 |
| 25 | 0.70 | 0.0 | 0.25 | 0.5 | 0 | 4.5 | 0.70 | 0.0 | 0.25 | 0.5 | 0 | 3.0 |
| June 11 | 0.00 | 2.0 | 0.00 | 1.5 | 0 | 4.5 | 0.00 | 2.0 | 0.00 | 3.0 | 0 | 2.5 |

Note. The figures in the body of the table are the % level of carbon dioxide maintained (treatment) and the consequent oxygen uptake rate in $\mu l$ $0_2$/g/hr.

Table 3 The effect of a range of carbon dioxide concentrations on the respiration rate of 1 g samples of re-wetted soil from diverse sources

| Type of soil | | | Effect of carbon dioxide* | | | | |
|---|---|---|---|---|---|---|---|
| Source** | Nature | *p*H | 0% | 1.7% | 5.6% | 7.0% | 9.2% |
| Lyngjorden | Sandy under *Calluna* | 4.00 | 4—5 | 0.0 | 0.0 | 0.0 | 0.0 |
| Sletten | F. Sandy, Grassland | 4.80 | 4 | 3.5 | 0.0 | | |
| Oakwood | F. Sandy, brown earth | 5.40 | 12 | 6.0 | 4,5 | 1.0 | 0.0 |
| Oakwood | H. Sandy, brown earth | 4.05 | 13 | 13.0 | 1.0 | 0.0 | |
| Oakwood | H. Sandy, brown earth | 4.05 | 13 | 13.0 | 2.5 | 0.0 | |
| Monsklint | Clay Grassland near chalk | 5.30 | 11 | 11.0 | 4.0 | 2.0 | |
| Monsklint | Clay Grassland near chalk | 5.30 | 13 | 5.0 | 5.5 | 2.0 | |

** The source of all samples except the last was within the Molslaboratoriet area in Jylland. Monsklint are in the island of Mon.

* The figure in the body of the table is the approximate oxygen uptake rate in $\mu l$/g/hr. For the last two soil types two samples were used.

In order to check whether the results obtained with the sandy soil beneath *Calluna* were peculiar to this soil or could be applied more generally to other soils, a small number of other samples were taken from a variety of habitats and subjected to the same treatment. The properties of the soils and their response to the different carbon dioxide levels are summarised in Table 3. The preliminary conclusion from these results appears to be that the sandy soil from Sletten (a sandy raised beach close to the Baltic shore and now covered with grasses used for grazing cattle) shows some inhibitory effect at 1.7% carbon dioxide. In the nearby somewhat sandy brown earth soils under oak, the F layer may have been slightly more susceptible than the H layer to carbon dioxide. The former showed 50% reduction at 1.7% carbon dioxide the latter at somewhere between 1.7% and 5.6%. Respiration stopped completely in both cases at about 7%. The soil derived from more alkaline clays under beech trees, close to the chalk cliffs at Mons klint reaches 50% respiration rate at about 5.6% carbon dioxide but is not completely stopped even at 7%. These higher figures correspond with the highest levels of soil carbon dioxide quoted in the literature. For example Russell and Appleyard (1915), Meyer and Schaffer (1954).

### 3.3. Experiment to determine the maximum carbon dioxide level attained above re-wetted soil in a confined vessels

Re-wetted "soil", all consisting of F layer material, from the same source as in the previous experiments, was used and experiments were conducted two weeks after wetting. The quantity of carbon dioxide contained in the air of the vessel and absorbed in the

Table 4 The level of carbon dioxide attained in closed (150 ml) vessels above re-wetted soil when absorbed and analysed on successive dates

| Days after commencement | 2 | 4 | 7 | 9 | 10 | 12 |
|---|---|---|---|---|---|---|
| Concentration of $CO_2$ (%) | 0.32 | 0.68 | 0.65 | 0.68 | 1.18 | 1.20 |

Table 5 Measurements of carbon dioxide concentration in soil air determined by means of polythene tubes (Results are expressed as % $CO_2$)

| Method | Exposure Time (days) | Position of tube | | | |
|---|---|---|---|---|---|
| | | Shallow | | Deep | |
| Syringe | 2 | 0.075 | 0.075 | 0.175 | — |
| Syringe | 9 | 0.280 | 0.250 | 0.250 | — |
| Bicarbonate | 9 | 0.130 | 0.100 | 0.130 | 0.160 |

alkali was determined by titration. This was expressed as percentage concentration of the gas in the tubes. The volume of the vessels was determined previously. The results (Table 4) were taken to indicate that the microorganisms in the soil in question probably cease aerobic respiration at a carbon dioxide concentration of rather more than 1.20%.

### 3.4. Field determination of carbon dioxide levels

On 9 November 1966 four air-filled and four bicarbonate filled polythene tubes of the kind described above were exposed beneath *Calluna vulgaris*; two of each pair as close to the soil/litter interface as possible and two more at 5 cm depth. The soil was wet after rather heavy rain during the previous twenty-four hours (16 mm) and the temperature was approximately 7 °C.

The air-filled tubes were sampled by the syringe method and the results in Table 5 were obtained. (It will be noted that the syringe method could be used repeatedly whilst the bicarbonate methodes could only be read once.) These results are not very adequate in themselves and it was felt that the extent to which the extra dilution of soil air from above might have occurred was hard to determine. Nevertheless, they indicate a maximum level of about 0.25% carbon dioxide at both depths.

## 4. Discussion

All of the methods described have their imperfections. The laboratory methods, on account of the uncertainty of extrapolation from undisturbed soil to artificial materials and the field method due to the uncertain effects of disturbance. Nevertheless, when taken together it is considered that positive evidence is provided for the occurrence of inhibition of respiration by carbon dioxide in the soil atmosphere.

The flattening off of the respiration/temperature curve at about 15 °C for soil cores recently removed from the field and enclosed in a glass tank as compared with others which are ventilated suggests the operation of an inhibitory effect. This is not necessarily, of course, due to the build up of carbon dioxide.

The consistent inhibition of respiration in reconstituted, re-wetted soil by carbon dioxide buffers and in the absence of a serious decrease in oxygen or accumulation of toxic products is established by the Warburg respirometry experiments. This effect occurs in the region of 0.7% carbon dioxide or lower and the restoration of respiration by a return to zero carbon dioxide indicates a susceptibility of the sandy soil in question. The failure of other soils to show this phenomen at such low carbon dioxide levels,

but its existence at levels ten times as high appears to indicate that the effect is a property of soil type and is presumably related to the type of microflora that can exist in particular habitats. It would appear that, in the acid sandy soil below *Calluna* they are particularly susceptible. This finding is supported by the independent evidence based on plate cultures quoted by the mycologists in the literature and to some extent by the intermediate position of the sandy soil beneath grassland at Sletten. The carbon dioxide accumulation experiment indicates that the organisms concerned ceased to metabolise entirely above about 1.2% carbon dioxide and this sets an upper limit to all activity.

The experiments on the carbon dioxide concentration in the soil atmosphere were unfortunately confined to the autumn period when metabolism is likely to be low and are subject to the possibility that dilution of soil air from above would lead to low results. However, they do set a lower level of about 0.25% carbon dioxide as a "working level" under natural conditions. This corresponds fairly closely with the values at which the inhibitory effect of soil carbon dioxide is thought to be beginning to operate.

Thus, it is concluded that soil carbon dioxide concentration of the soil air in light sandy soils at Molslaboratoriet can and does restrict the metabolic rate of the microorganisms which are mainly active in these soils. It remains certain, of course, that the gas concentration in the immediate vicinity of bacteria and fungi and also the carbon dioxide level in the absorbed water would be very different from that in the generally-circulating soil air. The concentration in such places is, however likely to be related to, and higher than, that in the air. It follows that this must be a factor in reducing the rate of decomposition of plant litter. The likelihood is that this factor operates at times of year which are otherwise favourable to decomposition and this is supported by evidence (already mentioned at the outset) of restricted metabolic activity in summer and at around midday. The coincidence of Warburg respirometer results with the known maximum carbon dioxide levels for other types of soils than the sand also suggests that inhibition of activity by carbon dioxide accumulation may not be confined to the sandy soils which were briefly studied here but could on the other hand be a widespread phenomenon. Some support for the results reported here comes from JENSEN (1967), who cultured wood-decaying fungi in atmospheres of reduced oxygen and increased carbon dioxide and demonstrated that the levels of both gases, at which growth was suppressed, corresponded to those which have been reported in the literature as occurring within their natural habitats.

## 5. Acknowledgements

I wish to thank particularly Professor Dr. H. M. THAMDRUP and the trustees of Aarhus Naturhistorisk Museum for facilities and support whilst working at Molslaboratoriet. I am most grateful to Professor THAMDRUP for his interest and encouragement and also to FRK. SNILDE PARSBO and Miss JILL SHEPPARD and members of my own family for meticulous care and much assistance with reading respirometers and collecting other data.

## 6. Summary · Zusammenfassung

During studies on carbon dioxide evolution from a sandy heathland soil in Mols (Denmark) the possibility that the accumulation of $CO_2$ in soil is linked with a limitation of microbial respiration rate was raised. This possibility was tested by four independant methods: (1) a laboratory method using intact cores, (2) using air dried, re-wetted soil in a Warburg respirometer in the presence of $CO_2$ buffers (3) measurement of maximum $CO_2$ accumulation in confined vessels and (4) field measurements of $CO_2$ in the soil.

The different techniques all point to the existence of an inhibitory effect at levels below 1% $CO_2$ in the particular sandy soil under *Calluna*. The same methods with other soils give results consistent with the generally accepted view that such inhibition does not occur below 10% $CO_2$. Support for existence of the phenomenon is quoted from the literature.

[Hemmeffekte von $CO_2$ auf die mikrobielle Aktivität in Böden]

Während der Untersuchungen über die $CO_2$-Freisetzung aus sandigen Heideböden in Mols (Dänemark) wurde die Möglichkeit, daß die Akkumulation von $CO_2$ mit einer Beschränkung der mikrobiellen Respiration verbunden ist, entdeckt. Diese Möglichkeit wurde durch vier voneinander unabhängige Methoden geprüft: (1) durch eine Laboratoriumsmethode, unter Verwendung von intakten Bodenausstichen, (2) durch Verwendung von luftgetrockenetem, wiederbefeuchtetem Boden in einem Warburg-Respirometer, unter Zusatz eines $CO_2$-Puffers, (3) durch Messung der maximalen $CO_2$-Akkumulation in geschlossenen Gefäßen und (4) durch Freiland-Messungen der $CO_2$-Freisetzung aus dem Boden.

Die mit verschiedenen Techniken erzielten Ergebnisse wiesen auf die Existenz eines Hemmeffektes (in einem ziemlich sandigen Heideboden) bei Konzentrationen unter 1 % hin. Die gleichen Methoden ergaben bei der Untersuchung anderer Böden Resultate, die mit der allgemeinen Annahme, daß derartige Hemmeffekte nicht unterhalb von 10 % $CO_2$ auftreten, übereinstimmen. Hinweise auf die Existenz des in Frage stehenden Phänomens werden aus der Literatur zitiert.

## 7. References

Burges, A., and E. Fenton, 1953. The effect of carbon dioxide on the growth of certain soil fungi. Trans. Brit. mycol. soc. **36**, 104–108.

Birch, H. F., and M. T. Friend, 1956. Humus decomposition in East Africa soils. Nature, London, **178**, 500–501.

Chase, F. E., and P. H. H. Gray, 1953. Use of the Warburg respirometer to study metabolic activity in soil. Nature, London, **171**, 481.

Jensen, K. F., 1967. Oxygen and carbon dioxide affect the growth of wood-decaying fungi. Forest Science **13**, 384–389.

Macfadyen, A., 1970. Simple methods for measuring and maintaining the proportion of carbon dioxide in air, for use in ecological studies on soil respiration. Soil Biol. Biochem. **2**, 9–18.

Macfadyen, A., (In prep.). Soil carbon dioxide production as an index of soil metabolism.

Meyer, L., und G. Schaffer, 1954. Atmungskurven des Bodens unter dem Einfluß von Düngung und Bewachsung. Landwirtsch. Forsch. **6**, 81–95.

Russell, E. J., and A. Appleyard, 1915. The atmosphere of the soil, its composition and causes of variation. J. agric. Sci. **7**, 1–48.

Umbreit, W. W., R. H. Burris and J. F. Stauffer, 1957. Manometric techniques. Burges, Minneapolis. 338 pp.

Address of the author: Prof. Dr. Amyan Macfadyen, School of Biological and Environmental Studies. The New University of Ulster, Coleraine, County Londonderry, Northern Ireland.